

CHANGES IN ABUNDANCE OF HARBOR SEALS IN MAINE, 1981–2001

JAMES R. GILBERT

Wildlife Ecology, University of Maine, Orono, Maine 04469, U.S.A.
E-mail: james.gilbert@umit.maine.edu

GORDON T. WARING

Northeast Fisheries Science Center, National Marine Fisheries Service,
166 Water Street, Woods Hole, Massachusetts 02543, U.S.A.

KATE M. WYNNE

University of Alaska, Sea Grant, Marine Advisory Program,
118 Trident Way, Kodiak, Alaska 99615, U.S.A.

NIKOLINA GULDAGER¹

Wildlife Ecology, University of Maine, Orono, Maine 04469, U.S.A.

ABSTRACT

Aerial counts of harbor seals (*Phoca vitulina concolor*) on ledges along the Maine coast were conducted during the pupping season in 1981, 1986, 1993, 1997, and 2001. Between 1981 and 2001, the uncorrected counts of seals increased from 10,543 to 38,014, an annual rate of 6.6 percent. In 2001 30 harbor seals were captured and radio-tagged prior to aerial counts. Of these, 19 harbor seals (six adult males, two adult females, seven juvenile males, and four juvenile females) were available during the survey to develop a correction factor for the fraction of seals not observed. The corrected 2001 abundance estimate was 99,340 harbor seals. Productivity in this population has increased since 1981 from 6.4% pups to 24.4% pups. The number of gray seals (*Halichoerus grypus*) counted during the harbor seal surveys increased from zero in both 1981 and 1986 to 1,731 animals in 2001.

Key words: harbor seal, *Phoca vitulina*, population estimation, distribution, New England, gray seal, *Halichoerus grypus*.

The harbor seal (*Phoca vitulina*) is the most widely distributed phocid seal in the North Atlantic (Thompson *et al.* 1997). The western North Atlantic subspecies of harbor seal (*P. v. concolor*) is distributed from the eastern Canadian Arctic and Greenland south to southern New England and New Jersey (Boulva and McLaren 1979, Katona *et al.* 1993). The species is the most abundant phocid in New England

¹ Current address: National Park Service, 201 First Avenue, Fairbanks, Alaska 99701, U.S.A.

coastal waters (Payne and Selzer 1989). The gray seal (*Halichoerus grypus*) is also found year-round in New England.² Harp seals (*Pagophilus groenlandicus*) and hooded seals (*Cystophora cristata*) are regular winter visitors to the Gulf of Maine (Stevick and Fernald 1998; McAlpine and Walker 1999; McAlpine *et al.* 1999; Harris *et al.* 2001, 2002), with ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) being rare winter visitors.

Historically, harbor seals were killed by fishermen and others as they were considered a nuisance and a competitor for fish. Beginning in colonial times New England communities enacted intermittent bounty programs to control seal populations, which resulted in local extirpation (Katona *et al.* 1993). However, since 1972 seals have been protected in U.S. waters under the Marine Mammal Protection Act.

In colonial times seals were likely abundant, as early explorers described seals as "teeming" along the coast of Maine, and both harbor seals and gray seals were significantly represented in middens of coastal native settlements (Speiss and Lewis 2001). Richardson³ estimated there were 5,000 seals on Maine's coast from aerial counts conducted throughout the summers of 1973 and 1974. Between 1981 and 1997, we have conducted periodic counts of harbor seals at its haul-out sites in Maine for the purpose of obtaining a minimum population number.⁴

Estimation techniques for phocid seals have advanced over the past several decades. Early estimates of harbor seal numbers were based on counts of seals observed on land (or ice). Pitcher and McAllister (1981) noted that these counts were variable, and suggested that replicate counts were necessary to achieve some reliability. Even under ideal conditions, not all seals are out of the water (Schneider and Payne 1983, Watts 1996). Counts were often taken during pupping or molting when a larger fraction of the seals were hauled out (Heide-Jørgensen and Härkönen 1988, Thompson and Harwood 1990, Stobo and Fowler 1994, Reijnders *et al.* 1997, Frost *et al.* 1999, Huber *et al.* 2001).

To reduce variability in seal counts, several adjustment and correction techniques have been used. The first type of adjustment is asynchronous, in that estimation of the correction is independent of the estimate of the numbers out. Frost *et al.* (1999) considered trends in numbers most important, and adjusted replicate counts of seals on a sample of sites to an average count using environmental variables as cofactors. Boveng *et al.* (2003) adjusted replicate trend counts to a maximum count using environmental variables and then corrected this using data from satellite tagged animals to estimate the fraction of the population hauled out under ideal conditions (Simpkins *et al.* 2003).

The second type of adjustment is synchronous, in that data on the fraction out of the water are collected at the same time as the seals are counted. Ries *et al.* (1998), Huber *et al.* (2001), and Jeffries *et al.* (2003) used the fraction of radio-tagged seals located at the time counts were conducted to estimate the fraction of the seal population out of the water.

² Rough, V. 1995. Gray seals in Nantucket Sound, Massachusetts, winter and spring, 1994. Final report to U. S. Marine Mammal Commission, Contract T10155615. National Technical Information Service Publication PB95-191391. 28 pp.

³ Richardson, D. T. 1976. Assessment of harbor seal and gray seal populations in Maine 1974-1975. Report to U. S. Marine Mammal Commission Contract No. MM4AC009. Available from J. Gilbert.

⁴ Gilbert J. R., and N. Guldager. 1998. Status of harbor and gray seal populations in Northern New England. NMFS/NER Cooperative Agreement 14-16-009-1557 Woods Hole, MA. Available from NEFSC, Woods Hole, MA.

Aerial surveys to estimate population size have been conducted either during the molting season or the pupping season. Recently, Daniel *et al.* (2003) showed that male and female harbor seals in Alaska have different molting times, and molting times shift from year to year. Counts during pupping season are sensitive to the timing of the survey relative to peak pupping, and the time of peak pupping can vary from year to year (Bowen *et al.* 2003a, Dubé *et al.* 2003). During the pupping season the population segregates by sex and age (Kovacs *et al.* 1990).

Conducting surveys within 2 h of either side of the time of low tide has become standard as this is when most seals are expected to be hauled out (Watts 1996). When possible, surveys are conducted when the time of low tide occurs near midday, as time-of-day influences haul-out numbers. Other factors affecting seal counts include temperature, height of tide, and wind (Frost *et al.* 1999, Boveng *et al.* 2003). Several studies (Thompson *et al.* 1997, Härkönen *et al.* 1999, Härkönen and Harding 2001, Huber *et al.* 2001, Boveng *et al.* 2003) have also found that the fraction of time a harbor seal spends out of water varies with the sex and age of the animal.

The objectives of this study were to: (1) conduct replicate aerial surveys to obtain counts of harbor seals hauled out during the 2001 pupping season and correct the counts with an estimate of the fraction of the population in the water that was not observed, and (2) compare these results with earlier counts to get a general sense of population trend and changes in coastal distribution.

METHODS

Study Area

The study area extended throughout the coastal waters of Maine from the Maine–New Hampshire border to the Canada–United States border (Fig. 1). During the pupping season, New England's harbor seal population is found primarily in this area. In the winter a significant number of harbor seals are found from Cape Cod, Massachusetts, to Long Island, New York, although some remain in Maine waters (Payne and Selzer 1989). In recent years more seals seem to be remaining in the Cape Cod area during summer.⁵ Some individuals also are in pelagic waters of the Gulf of Maine during pupping, as evidenced from the bycatch of harbor seals in gill nets.⁶

Maine's 5,600 km of coastline between Cobscook Bay on the U.S.–Canadian Border and the Isles of Shoals on the border with New Hampshire has many bays and over 3,500 islands and rock ledges (Fig. 1). From Cape Elizabeth south, the coast is primarily comprised of sandy beaches with few islands. North of Cape Elizabeth, the coast is primarily rock carved by glaciation into a complex coastline. Tide range varies from 2.6 m in South of Cape Elizabeth to 5.9 m in Cobscook Bay.

The larger islands are occupied by people year round, and additional islands have occupied dwellings in the summer. Fishing activity, especially the setting and recovery of lobster traps, occurs near these ledges and islands without undue disturbance of the seals. The coasts and adjacent waters are the focus of varied recreational activities that peak in July and August. Harbor seals and gray seals are found on

⁵ Personal communication from Belinda Rubinstein, New England Aquarium, Boston, MA, December 2003.

⁶ Williams, A. S. 1999. Prey selection by harbor seals in relation to fish taken by the Gulf of Maine sink gill net fishery. M.S. thesis, Wildlife Ecology, University of Maine, Orono ME. 622 pp.

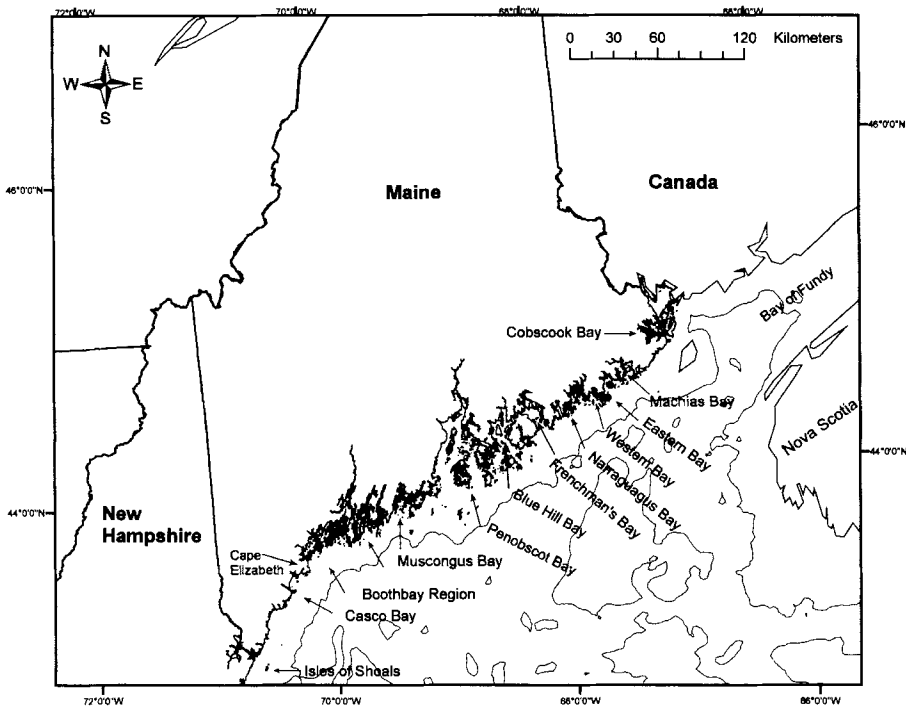


Figure 1. Locations of the bays along the Coast of Maine that were used to subdivide the seal survey study area. The 100-m depth contour is indicated in the Gulf of Maine.

ledges and islands that are not occupied by people. Many of these ledges are flooded at high tide.

Field Methods

We counted pups and adults from an island point overlooking several ledges in the Muscle Ridge area of Penobscot Bay on multiple occasions between 17 May and 28 June 1998. These data were used to identify the timing and length of the pupping season. We used this information as a guide to set the dates for the 2001 survey and interpret the results from earlier surveys.

All aerial surveys used similar procedures. These involved circling the haul-out sites at altitudes between 130 and 170 m and photographing the seals or conducting visual counts if there were few seals. All counts were accomplished within 2 h of either side of the time of low tide. During the flight one observer photographed seals on ledges and the second observer recorded the locations of photographs. In 2001 we also recorded the path of each flight with a GPS and downloaded these data to a mapping program (Maptech Ocean Navigator)⁷ for evaluations of the coverage each day. Prior to 1997, we used a single aircraft and surveyed ledges once, generally extending from Cobscook Bay to Cape Elizabeth or

⁷ Reference to brand names does not imply endorsement by NOAA Fisheries.

Table 1. Dates of surveys and regions examined in count of seals on the coast of Maine.

Year of survey	Dates	Region covered
1981	8–18 June	All of coastal Maine
1986	15–21 June	All of coastal Maine
1993	28 May–11 June	All of coastal Maine and Isles of Shoals
1997	27 May–4 June	All of coastal Maine and Isles of Shoals
1997 replicates	9–10 June	Segments of Penobscot Bay
2001 first survey period	16–20 May	Coastal Maine and Isles of Shoals except Cobscook Bay
2001 first period replicates	16–20 May	Isles of Shoals through Muscongus Bay
2001 second survey period	27 May–4 June	All of coastal Maine and Isles of Shoals
2001 second period replicates	2 May–1 June	Penobscot, Blue Hill, and Cobscook bays

the New Hampshire border (Table 1). In 1997, after we completed a single count of the seals on the entire coast, we replicated counts of a part of Penobscot Bay.

In 2001 we attempted to obtain replicate counts between 16 May and 4 June. Between 21 and 26 May, the time of low tide was too late in the evening or too early in the morning to survey effectively. We thus defined a first survey period and a second survey period to correspond to 16–20 May and 27 May–4 June flight windows, respectively.

On each survey day in 2001, one aircraft was dedicated to relocating radio-tagged seals. When seals were being counted from two other aircraft, we flew this aircraft over the general area where the tagged seals were located, taking 3.5–4 h to search the area once. At an altitude of 350 m, radios could be heard at least 8 km from the flight line.

In 1981 and 1986 we photographed seals with a 200-mm lens on ASA 400 35-mm slide film. We used a 300-mm lens in subsequent years. All rolls of 35-mm slides were processed and sequentially numbered for later identification.

We generally counted seals on slides twice or had two people count each slide at the same time. In 2001 we initially counted seals on all rolls of film once. From these data, we determined that numbers of seals counted were significantly higher during the second survey period than during the first survey period. To verify our slide counts for the second survey period, we recounted the slides from the second period. An individual scientist examined a group of photographs that covered a ledge or island. The counter first determined the minimum and maximum number of total seals on the ledge. The counter then determined the minimum and maximum numbers of pups and the minimum and maximum number of gray seals. The minimum and maximum numbers were then averaged and used as estimates for the number of pups, gray seals, and total seals. The number of harbor seals was then the difference between the average number of total seals and the average number of gray seals. If there were minimal (+2) differences between the counters' results, they were averaged. If the differences were large, the slides were counted a third time. Usually the difference was due to counting multiple images of the same group of seals. We used the average of two counts of the slides for analysis.

During the first survey period in 2001, all the regions except Cobscook and Machias bays were surveyed once (Fig. 1) and regions from Isles of Shoals to western Penobscot Bay were surveyed in a second replicate. In the second survey period, the entire coast from Isles of Shoals through Cobscook Bay was surveyed and Penobscot, Blue Hill, and Cobscook bays were surveyed twice (Fig. 1). In 4 h an aircraft could cover only part of the coast. In all the surveys, it would take at least 5 d to obtain one complete coastal count of harbor seals.

Prior to the survey effort in 2001, we captured harbor seals and attached two VHF transmitters to each animal to obtain a correction factor for the survey. Harbor seals were captured from 12 to 21 March 2001, in Chatham, Massachusetts and from 13 to 20 April in Rockland, Maine (Fig. 1). We used a seine net to capture the seals as described by Jeffries *et al.* (1993).

Two VHF transmitters were attached to each animal; one (Lotek model MBFT-5) was mounted on a flipper tag (Alflex)⁷ and a second (Telonics MOD-073)⁷ was glued to the lower back using 5-min epoxy (Fedak *et al.* 1983). These attachment locations allowed signal transmission when the seals were out of the water. Two VHF tags were affixed to each seal to estimate tag loss and to insure that the maximum number of seals had at least one operating radio.

Prior to the first aerial abundance survey in 2001, we conducted aerial flights during the first two weeks of May to relocate the tagged seals that had moved into or stayed in the survey area. We searched the entire coast of the study area for tagged individuals. We treated the set of seals located as the number available to be detected in deriving a correction factor for the abundance survey. We then monitored this set of radios for presence or absence during abundance surveys to determine the percentage of animals hauled out and available to be counted. After the survey, radio-tagged seals were located to determine their continued presence in the study area.

Sites near Brunswick Naval Air Station in the Casco Bay region were not observed because our aircraft were restricted from airspace near the facility. We did not fly up rivers (*i.e.*, beyond major road ways) as far as seals can go, and therefore seals at haul-outs that were far up rivers were not included in these results.

Estimation Procedure

The estimate of the harbor seal population abundance required estimates of the number of seals hauled out on land and a correction for those seals not observed. Because we wanted to compare our counts and distribution with those in previous surveys, we estimated the population size in each of several predefined regions, each being one or more physical bays in the study area (Fig. 1).

Estimation of the correction factor and its variance from the radio-tag relocations was accomplished using the approach of Huber *et al.* (2001) wherein the correction factor was calculated as:

$$(1/\hat{p}_d), \quad \text{where } \hat{p}_d \text{ is the fraction of radio tags located in day } d, \text{ and}$$

$$V(1/\hat{p}_d) = \frac{v(\hat{p}_d)}{\hat{p}_d^4}. \quad (1)$$

We estimated the fraction out of the water each survey day using the program MARK (White and Burnham 1999). We recognized that there were a variety of

cofactors that influenced the estimate of the fraction observed. We attempted to capture many of these by obtaining an estimate of the fraction available to be counted for each day when counts were conducted. As such, this procedure was "pooling robust" in the sense discussed by Burnham *et al.* (1980) and Buckland *et al.* (1993). Our estimation procedure was similar to that of Ries *et al.* (1998).

We divided the coast into regions (Fig. 1) to be able to monitor population changes on a finer scale. We defined our sample unit, a "region-unit," to be that portion of a region that was surveyed from one aircraft on a single day and from a second aircraft on the same or a different day. In situations where there was only one survey, the part of the region surveyed on a single day was the region-unit. Each region-unit had multiple haul-out sites. Because previous studies (*e.g.*, Boveng *et al.* 2003) showed that time of day was a significant co-factor, we estimated the correction factor (\hat{p}) and its variance for each day surveyed.

Each region-unit count (C_{iu}) was corrected for the proportion of radio-tagged seals observed on that day (d) as:

$$N_{iu} = C_{iu}(1/p_d). \quad (2)$$

We estimated the total population \hat{N} from the sum of all the corrected estimates over all replicates ($i = 1, 2$) and region-units ($u = 1, 41$),

$$\hat{N} = \sum_u \left(\frac{\sum_{i=1}^2 \hat{N}_{iu}}{r} \right), \quad (3)$$

where r is the number of replicates in a unit.

In the 24 region-units surveyed twice, each count was corrected then averaged to obtain an estimate for that unit. In the remaining 17 region-units that had only one survey, we used the corrected count from one survey as the estimate.

If the estimate for a region-unit was based on two corrected counts, its variance was:

$$V(\hat{N}_u) = \frac{\sum_{i=1}^2 (C_{iu}^2 \cdot V(1/p_d))}{2}. \quad (4)$$

In those instances when there was only one survey of a region-unit, we incorporated an average variance from the average coefficient of variation of the counts from those region-units surveyed twice. We estimated an average coefficient of variation for the uncorrected counts for those region-units with two counts to estimate the variation associated with a single count. The estimated variance for a single count in region, $c_u \cdot CV^2$, was incorporated into the estimate of variance for the corrected count for the region-unit as:

$$V(N_u) = (c_u \cdot \overline{CV})^2 \cdot (1/p_d)^2 + c_u^2 \cdot V(1/p_d). \quad (5)$$

The variance of the estimated total number was the sum of the variances of the corrected counts for each bay-unit:

$$V(\hat{N}) = \sum V(\hat{N}_u). \quad (6)$$

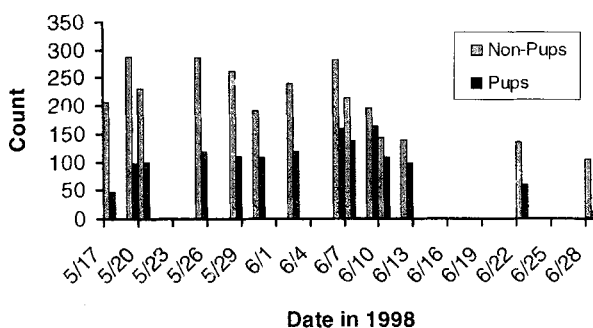


Figure 2. Daily counts of pups and non-pups of Muscle Ridge area of Penobscot Bay indicated that numbers of individuals that could be identified as pups declined in the middle of June 1998.

The confidence limits for each of the estimates followed Thompson *et al.* (1998:95):

$$\left[C + \frac{(\hat{N} - C)}{Q}, C + (\hat{N} - C) \cdot Q \right],$$

where

$$Q = \exp \left(t_{18df} \cdot \sqrt{\ln \left[1 + \frac{V(\hat{N})}{(\hat{N} - C)^2} \right]} \right), \quad (7)$$

and

$$C = \sum C_u, \quad \text{the total of the uncorrected counts.}$$

We compared the uncorrected counts to counts from aerial surveys conducted in previous years over the same areas. These earlier counts were not corrected for the number of seals not observed. Coast-wide aerial surveys were previously completed in May/June during pupping in 1981, 1986, 1993, and 1997. Procedures in these earlier aerial surveys were similar to those in 2001, with photographs taken of nearly all seal groups (occasionally we did not photograph single seals, but did include the count in the analysis). We did search all ledges and islands that we knew had seals previously and all ledges and islands that were similar to these in size and not occupied by humans. In preparation for this paper, we reviewed the original data to confirm previous summaries.

RESULTS

Between 17 May and 28 June 1998, we conducted low-tide counts of harbor seal pups and non-pups on 14 occasions at a set of ledges in the Muscle Ridge Area of Penobscot Bay. Pups comprised a maximum of 45% of the total seals on 9 June (Fig. 2). The number of pups declined sometime after 13 June. This effort roughly identified the extent of the pupping season (the earliest pup in Penobscot Bay was

Table 2. Number of locations of radio-tagged harbor seals during the first (16–20 May) and second (27 May–4 June) survey periods, 2001.

Tag number	Sex	Age ^a	Number of times located 17–20 May 2001 ^b	Number of times located 27 May–4 June 2001	Total locations
12	F	A	2	5	7
24	F	A	1	2	3
23	F	J	0	1	1
26	F	J	3	2	5
29	F	J	0	2	2
30	F	J	2	3	5
31	F	J	1	0	1
1	M	A	3	1	4
10	M	A	0	4	4
14	M	A	1	3	4
18	M	A	1	0	1
19	M	A	3	6	9
20	M	A	1	1	2
32	M	A	0	2	2
22	M	J	1	2	3
25	M	J	3	2	5
34	M	J	1	2	3
35	M	J	2	5	7
36	M	J	0	4	4
Total			25	47	72
Number of days			3	6	9
\hat{p}			0.439	0.412	0.421

^a A = adult, J = juvenile.

^b The area was not searched for radio-tagged seals on 16 May.

seen on 28 April), and these data were used to define the dates for the aerial counts in 2001 and to interpret previous counts.

In March 2001, 21 harbor seals were captured off Cape Cod, Massachusetts for radio-tagging. We attached a VHF transmitter to the rear flipper of 13 animals and a second transmitter to the lower back of 12 of these seals. In April 2001, we captured 18 additional harbor seals in Penobscot Bay, Maine and attached two radio tags to each of 17 of these animals.

Aerial flights were conducted on seven days in the first two weeks of May to relocate the radio-tagged seals. We located 19 of the 30 radio-tagged seals along the coast of Maine. These 19 radio-tagged seals included six adult males, two adult females, seven juvenile males, and four juvenile females. Seven of the 13 seals tagged on Cape Cod returned to Maine and were part of the sample. An additional seal (Tag Number 16) detected at Isles of Shoals was beyond our usual search range and was excluded. Flipper-tag mounted radios were not detected in nearly all instances when back tags were located; either the antennas broke or the tags were lost. Subsequently we used data only from the back-mounted radios.

We were able to locate radio-tagged seals during all days of the abundance survey except 16 May. Overall, we located an average 42% of the radioed seals each day during the survey (Table 2). The estimated probability of a seal being out of the water (\hat{p}) was not different between the first survey period (16–20 May) and the

Table 3. Comparison of numbers observed in the first survey period in 2001 (16–20 May) to numbers observed in the second survey period (27 May–4 June).

Region	First period		Second period	
	Non-pups	Pups	Non-pups	Pups
South of Cape	1,169	101	996	99
Casco Bay	1,841	320	2,599	720
Boothbay Region	2,722	299	3,152	400
Muscongus Bay	2,539	595	2,761	838
Penobscot Bay	5,259	557	6,341	2,102
Blue Hill Bay	4,595	517	5,942	2,517
Frenchman's Bay	1,603	106	1,777	507
Narraguagus	1,288	85	1,300	435
Western Bay	878	67	1,389	647
Eastern Bay	1,203	161	1,254	569
Machias Bay			1,077	399
Cobscook Bay			144	49
Total	23,097	2,808	28,732	9,282

second survey period (27 May–4 June) (Table 2), indicating that the haul-out behavior of seals was similar in both survey periods. Probabilities of individual seals being in the water did not differ significantly from a binomial distribution, indicating there was no over-dispersion in the data, although this was likely due to small number of individuals tagged and the number of days of observations. The correction factor for each day's count ranged from 1.90 to 2.71 in the first period and from 1.46 to 3.80 in the second period.

In the 2001 survey, 72.8 h were spent photographing seals on 222 36-exposure rolls of 35-mm slide film (79 rolls from the first survey period and 143 rolls from the second survey period). In the first survey period, a total of 25,905 harbor seals were counted in all regions except Machias and Cobscook bays, compared to 36,345 harbor seals in the second survey period for the same regions (Table 3). Fifty-eight percent of this difference (6,026 of 10,440 seals) was due to an increase in pup counts (2,808 *vs.* 8,834), and the rest from an increase in the numbers of non-pups. Because the number of observed harbor seals in the second period was greater than in the first period in nearly all the regions, but the fraction observed in the radio telemetry data was not statistically different between the two survey periods, we based the 2001 harbor seal population estimate on counts from the second period.

In the second survey period we observed an estimated 38,014 harbor seals in the study area between the Isles of Shoals and Cobscook Bay. This number included 9,282 pups. We corrected the observed counts to estimate there were 99,340 harbor

Table 4. Estimate of harbor seal numbers in Maine in 2001 from counts and corrections for fractions not observed.

	Total counted	Corrected estimate	Variance of corrected estimate	Lower 95% confidence limit	Upper 95% confidence limit
Harbor	38,014	99,340	81,297,443	83,118	121,397
Pups	9,282	23,722	5,159,240	19,911	28,900
Non-pups	28,732	75,618	50,214,178	63,655	91,678

Table 5. Numbers of harbor seal pups and non-pups and gray seals observed in aerial surveys along the Coast of Maine from late May through mid-June.

Region	1981	1986	1993	1997	2001
South of Cape Elizabeth	272	346	942	1,733	996
Casco Bay	724	742	1,971	2,063	2,599
Boothbay region	900	1,837	2,228	3,284	3,152
Muscongus Bay	824	568	1,912	1,825	2,761
Penobscot Bay	2,797	2,281	7,011	4,732	6,341
Blue Hill Bay	1,948	2,305	5,526	5,350	5,942
Frenchman's Bay	816	504	972	1,364	1,777
Narraguagus region	675	848	1,207	1,287	1,300
Western Bay	371	498	1,050	1,220	1,389
Eastern Bay	162	766	1,108	1,390	1,254
Machias Bay region	268	389	1,199	1,249	1,077
Cobscook Bay region	110	143	155	186	144
Total non-pups	9,867	11,227	25,281	25,683	28,732
South of Cape Elizabeth	17	47	29	53	99
Casco Bay	33	136	231	314	720
Boothbay region	33	101	136	240	400
Muscongus Bay	36	60	256	262	838
Penobscot Bay	159	335	1,038	1,167	2,102
Blue Hill Bay	233	422	1,210	1,409	2,517
Frenchman's Bay	43	36	144	191	507
Narraguagus region	42	118	226	266	435
Western Bay	54	146	326	411	647
Eastern Bay	9	224	308	598	569
Machias Bay region	13	64	314	427	399
Cobscook Bay region	4	24	39	57	49
Total pups	676	1,713	4,257	5,395	9,282
Total harbor seals	10,543	12,940	29,538	31,078	38,014
Total gray seals	0	0	597	100	1,731

seals in the study area in late May and early June, 2001. The 95% confidence limits on this estimate were 83,118 to 121,397 (Table 4).

From 1981 to 2001, the number of seals observed in aerial surveys along the coast of Maine has increased from 10,543 to 38,014 animals, or approximately 3.6 times, just over 6.6% per year (Table 5). The number of pups observed has increased 14% per year between 1981 and 2001 (Table 5), while the abundance of non-pups increased 5.5% per year. Of these, 75,618 were non-pups. The percentage of pups in the population increased from 6.4% in 1981 to 24.4% in 2001.

The increase in harbor seal abundance has not been consistent throughout the study area (Table 5). Seal numbers in the Machias and Cobscook Bay regions appear to be no longer increasing. The Penobscot and Blue Hill Bay regions consistently have the most harbor seals and harbor seal pups. South of Cape Elizabeth few pups are born. Over 29% of the seals were pups in Western Bay, Eastern Bay, and the Blue Hill regions.

As the numbers of harbor seals have increased, the numbers of ledge and island sites used by harbor seals has also increased (Table 6) from 336 ledges in 1981 to 566 ledges in 2001. Although the number of sites used by all seals has not increased since 1993, the number of these sites used for pup rearing continues to

Table 6. Number of ledge and island sites occupied by harbor seals in Maine from 1981 to 2001.

Region	1981	1986	1993	1997	2001
Sites with harbor seals					
South of Cape Elizabeth	13	11	16	18	18
Casco Bay	26	22	41	33	43
Boothbay region	15	15	23	32	26
Muscongus Bay	28	21	44	44	47
Penobscot Bay	80	72	148	138	125
Blue Hill Bay	75	54	123	113	107
Frenchman's Bay	23	10	26	25	28
Narraguagus region	24	24	38	33	36
Western Bay	19	18	30	28	36
Eastern Bay	9	13	29	27	35
Machias region	14	15	37	34	41
Cobscook Bay	10	10	19	16	25
Total	336	285	574	541	566
Sites with harbor seal pups					
South of Cape Elizabeth	6	6	10	8	17
Casco Bay	13	18	32	26	37
Boothbay region	13	9	17	21	22
Muscongus Bay	17	12	32	27	40
Penobscot Bay	49	45	112	92	113
Blue Hill Bay	45	39	97	91	101
Frenchman's Bay	13	8	23	19	27
Narraguagus region	12	22	28	26	34
Western Bay	10	15	25	26	33
Eastern Bay	5	11	23	26	34
Machias region	5	7	23	26	36
Cobscook Bay	4	7	12	9	19
Total	186	193	424	389	496

increase. In 2001, 84.6% of the sites included pups, varying from 79% of the sites in Cobscook Bay Region to over 97% of the sites in the Eastern Bay Region.

The number of gray seals observed during the May–June surveys has also increased in the last 20 yr from 597 in 1993 to 1,731 in 2001 (Table 5). Prior to 1993, we did not observe gray seals in our aerial counts, although gray seals were observed by Richardson in the summers of 1974 and 1975.³

DISCUSSION

We obtained data for a correction to our observed counts at the same time as we were making counts of seals, following the procedures of Ries *et al.* (1998) and Huber *et al.* (2001). By correcting each day's count for the fraction of radio-tagged seals located, this procedure automatically captures the effect of temperature, wind, time of low tide, and other covariates. In contrast, other researchers (Frost *et al.* 1999, Boveng *et al.* 2003) collect data in order to predict the effect of each covariate on haul-out frequency. This allows counts to be conducted asynchronously from

collection of data on how the fraction hauled out is influenced by weather and time-of-day variables. Our approach, with synchronous collection of count and haul-out frequency data, does not require extensive collection information on covariate effects.

The average correction (2.58) for our counts is larger than in other studies during the pupping season. We located an average of 42% of our radio-tagged seals each day. Pitcher and McAllister (1981) located 50% of their tagged individuals, while Huber *et al.* (2001) observed 54%–74% of the seals they radio-tagged. This could be because seals in New England haul out less frequently or because our tagged sample misrepresented the sex and age distribution in the population. Females, especially adults, were underrepresented in our tagged sample, and sex and maturity have been shown to be significant factors influencing the proportion of the time seals spend on land during the pup rearing season (Thompson *et al.* 1997, Huber *et al.* 2001). However, we did not see any tendency for adult females in our sample to be out more frequently than other age and sex categories. The two adult females were located on three and seven of the survey days (Table 2). A larger sample size would be required to distinguish any existing differences in haul-out tendencies among sex and age classes of harbor seals in Maine. We also recognize that if there are sex and maturity differences that affect the proportion of low tides that a harbor seal is out of the water, unbiased application of these correction factors requires knowledge of the sex and age distribution in the population (Härkönen *et al.* 1999).

However, the average correction factor could be representative of seal behavior in the area. The sites that the harbor seals select in coastal Maine waters are often flooded at high tides. Seals, including females with pups, that use these sites, enter the water at least twice a day. Even on those sites that are not flooded at high tides, most seals enter the water.

We tagged harbor seals in Cape Cod, Massachusetts, approximately 2 mo before our counts began in Maine, both because we had reason to believe a fraction of those seals would return to Maine and because we did not believe we could capture enough seals in Maine before the survey. Harbor seals are found along the coast of Southern New England in the winter (Payne and Seltzer 1989) but not at other times of the year. Rosenfeld *et al.* (1988) speculated seasonal movement from the Bay of Fundy to southern New England because declines in numbers in one area correlated with increases in the other. We anticipated that a fraction of the seals tagged in Massachusetts would return to Maine. In April 1999 our tests of our efficiency in capturing seals on the rocky ledges of Maine indicated that we would not capture and radio-tag enough individuals if we worked only in this area. Five of the 17 seals tagged in April in Maine were not located in May prior to or during the survey in 2001. Possibly they lost their radio tags but more likely they were not in the area. Once the first survey began, no additional radio-tagged animals were located.

We based our estimates on data collected between 27 May and 4 June, even though counts at a series of ledges in 1998 indicated that counts beginning 16 May would be equivalent (Fig. 2). In the second survey period, there were significantly more pups observed than in the first, and this increase occurred in all regions excepting the most southerly. We also noted that the numbers of non-pups observed in the second survey period was higher than in the first period (Table 3). Most likely this increase was because additional seals moved into the area, likely from Southern New England. This difference could also be because of inherent variability in the counts and was therefore due to chance. However, excepting in the most southerly region (south of Cape Elizabeth), counts in the other regions consistently increased.

We have corrected counts of pups for the fraction not seen (Table 4). A pup is difficult to distinguish from a juvenile seal on a picture unless it is associated with a female seal. Our counts of pups were generally limited to those individuals that were immediately adjacent to an adult, either oriented parallel when resting or perpendicular when nursing. We are correcting for pups associated with females, therefore our counts are probably underestimating the numbers of pups. Our observations indicate a nursing pup generally accompanies the female into the water, but a weaned or abandoned pup remains out of the water more. We are therefore correcting the count of nursing pups. A more complex model of pupping is necessary to account for the weaned and abandoned pups.

We did not attempt to correct seal counts obtained prior to 2001, instead choosing to compare observed counts over years. We recognize that factors that would influence the observations are not accounted for, but believe that comparisons are valid because of the magnitude of the differences and the relative consistency of survey dates. In 1997 replicate counts on 31 May, 9 June, and 10 June of an area in Penobscot Bay did not differ. The observations taken in 1998 (Fig. 2) also do not indicate a decline in variability. Prior to 2001, no counts were taken before 27 May. Some of the observations taken in 1986 may be near the end of the pupping season, but we include them for reference. In all years, counts were taken over 4–5 d, generally within a tidal cycle. Thus, in each year, a mix of morning, midday and late afternoon tides were included in each survey. Therefore the counts are generally comparable.

The population of harbor seals in Maine has increased since the passage of the Marine Mammal Protection Act in 1972. Richardson³ counted 5,785 seals in 1972 and 1973, but the counts were conducted from May through August over two years. The number of harbor seals observed in 2001 was 3.6 times that in 1981. If pups are excluded, the increase was from 9,867 to 28,732, an increase of 5.5% per year. Some regions appear to not have increased since 1997 or have increased only minimally. Those regions from Eastern Bay to the Canadian Border did not change, perhaps implying more mortality or less productivity, and a separate stock structure.

The percent of pups increased from 6.4% in 1981 to 24.4% in 2001. In a stable population of harbor seals, pups are presumed to be 20% of the population (Bigg 1969). We believe our observation of 24.4% pups in 2001 to be real, but do not believe that the high percent of pups implies anything about the dynamics. Härkönen *et al.* (2002) noted that the presumption of 20% assumes a stable age structure and population.

The relatively high percent of pups might also be explained by fewer non-pupping females and non-breeding males in the study area. In some regions, notably Blue Hill, Western and Eastern bays, pups were 30% of all seals. These regions have consistently had a high percentage of pups between 1981 and 2001. The Penobscot and Blue Hill bay regions are the center of harbor seal production in Maine, producing approximately 50% of the pups each year. Pups were at least 20% of the count in all regions except south of Cape Elizabeth and the Boothbay Region (Table 5).

As the harbor seal population has grown, the number of ledges used by harbor seals during the pupping season increased (Table 6) then leveled at around 550 sites. The number of those sites used for pupping has increased, and in some regions, nearly all ledges have mother-pup pairs. If we had adopted trend counts in 1981 to monitor the harbor seal population, we would have missed some of the increase in the population size. This would lead us to recommend that exploratory surveys to identify any new haul-out sites should be incorporated into continuing trend counts.

Gray seals were observed during these surveys mixed with harbor seals or as separate groups. Aggregations of gray seals have been observed in consistent locations from survey to survey, but small numbers were also seen mixed with harbor seals during the 2001 survey. Bowen *et al.* (2003b) document a continuous increase in gray seal numbers on Sable Island, Nova Scotia, beginning in the 1960s. In 1997 an estimated 25,400 gray seal pups were born on Sable Island, making it the world's largest gray seal colony. Recently, gray seal numbers at a relic pupping site in the Cape Cod Region have begun to increase.⁸ Likely the gray seals we are observing originate at Sable Island, although genetics evaluations are needed to confirm this.

The 99,340 harbor seals (or 75,618 non-pups) in the New England population is one of the largest. Olesiuk *et al.* (1990) estimate a population of over 80,000 in British Columbia. The Coast of Maine extends about 250 km from New Hampshire to New Brunswick, a distance similar to that in southeastern Alaska from border with Canada to Cape Fairweather. Yet the population in Maine is at least double the 1998 estimate of 37,350⁹ for Southeastern Alaska. A possible reason for the large number of seals in Maine is that the population exploits a larger area seasonally, and has available to it a large expanse of habitat with water depths less than 100 m (Fig. 1). Harbor seals have been bycaught in ground fish gill nets in the Gulf of Maine⁶ and regularly are observed on haul-outs on Cape Cod and south in the winter months.

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⁸ Personal communication from Stephanie Wood, Biology Department, University of Massachusetts, Boston, MA, November 2003.

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